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Specialization and phyletic trends of sweetness reception in animals*

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Abstract: During the last decades, the comparison in various animal species of their gustatory responses to compounds eliciting a sweet taste in humans has extended our knowledge of the great biodiversity of the taste responses and evidenced some specialization and/or phyletic trends within species. Our interest was focused on responses to natural sugars, polyols, and naturally occurring sweeteners, but also on various artificial sweetening compounds, including the very powerful guanidine sweeteners. New results obtained with kangaroos—which originated about 130 MYA—have shown that their sweetness receptor is not designed to taste any of the artificial sweeteners tested. Therefore, the ability to taste complicated artificial sweeteners must have evolved later in higher developed mammals, about 100 million years ago.

INTRODUCTION

Fifty years ago [1], it was commonly suspected that animals share humans' taste world. But the fallacy of this contention was rapidly evidenced when the comparative gustatory responses in various animal species to compounds, sweet to humans, was studied. We can cite among the species I personally tested, fishes [2], hedgehogs [3], tree shrews [4], various primates [5–7], elephants [8], horses [3], cows [3], sheep [3], pigs [9,10], dogs, cats, mice, birds, reptiles, and, more recently, kangaroos. The observed biodiversity for the sweet taste among species may be considered as the result of two main evolutionary forces: specialization and phyletic trends. Specializations may be considered as minor variations resulting from adaptation to the different habitats of animals belonging to a species or closely related species/genera. Phyletic trends are milestones or major steps that occurred during the evolution progress leading to a higher grade within the evolution of species.

CONTEXTS AND RELATIONSHIPS

The gustatory sense is the last control before ingestion for discrimination of foods, the sweet taste being related to an acceptance, by opposition to the bitter taste rather related to a rejection [3]. Generally, animals' feeding habits and behavior may be classified in various categories such as carnivorous, omnivorous, phytophagous, etc. [11], but many species are not highly restricted in their natural diets. Daily and/or seasonal variations sometimes considerably shift feeding habits.

An example of specialization may be seen with some insect species such as flies [12], honey bees [12], and ants [13,14] (Table 1). For the tested polyols and carbohydrates, all known to be sweet to humans (except methyl-ß-D-glucopyranoside), the fly *Calliphora erythrocephala* (Diptera) has a pref-

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Table 1 Gustatory responses of some insect species, flies (*Calliphora*), ants (*Myrmica*, *Lasius*), and honey bees (*Apis mellifica*) to various polyols and carbohydrates [12–14] (+ means that the compound elicits a gustatory preference over water, – an indifference or a rejection).

Compounds	*Calliphora erythrocephala*	*Myrmica rubra*	*Lasius niger*	*Myrmica rubida*	*Apis mellifica*
Polyols					
Erythritol		–	–	–	–
Mannitol	+	+	–	–	–
Sorbitol		+	+	–	–
Dulcitol	+	–	–	–	–
Heterosidic carbohydrates					
Methyl-α-D-glucopyranoside	+	+	+	+	+
Methyl-ß-D-glucopyranoside			–		–
Monosaccharides					
D-Arabinose	+	–	–	–	–
L-Rhamnose	+	+	–	–	–
D-Glucose	+	+	+	+	+
D-Fructose	+	+	+	+	+
D-Galactose	+	+	–	–	+
D-Mannose	+	+	–	–	–
Oligosaccharides					
D-Sucrose	+	+	+	+	+
D-Maltose	+	+	+	+	+
D-Lactose	+	–	–	–	–
D-Melezitose	+	+	+	+	+
D-Raffinose	+	+	+	+	–
Total	14	12	8	7	7

erence for 14 compounds, the ant *Myrmica rubra* (Hymenoptera) for 12, the ant *Lasius niger* (Hymenoptera) for 8, the ant *Myrmica rubida* and the honey bee *Apis mellifica* (Hymenoptera) for only 7 compounds.

Interestingly, *Calliphora* and *Myrmica rubra,* which display preferences for a larger number of the compounds tested, are classified, regarding their main feeding habits, in the omnivorous group. The other three insect genera are more specialized for their feeding sources. For example, *Myrmica rubida* is carnivorous, while the honey bee is rather phytophagous and is specialized in the consumption of some specific plant nectars. In a discussion at an ECRO-Symposium in 1979, Schoonhoven [15] already mentioned, that in insects there are no two species with a completely identical sensory system. Apparently, the chemosensory system is very flexible and well adapted to the type of food and ecology of that particular species. Even insects that are so closely related that taxonomists can hardly distinguish them, but which live on different food plants, show striking differences [16].

Among the monosaccharide derivatives examined it is interesting to note that the methyl-α-D-glucopyranoside is sweet to flies, ants, honey bees, (Table 1), and pigs, as well as to humans [9]. Conversely, methyl-ß-D-glucopyranoside, which is not sweet to humans, gives negative responses in pigs, honey bees, and ants. That only the α-anomer is effective and not the ß-anomer seems to be an important feature for the heterosidic carbohydrates among the species tested. K. von Frisch discussed this fact previously in honey bees [12].

Let's have a look at carnivores: with a two-choice preference method the responses in cats (n = 18; in three groups) and dogs (n = 33; in five groups) were evaluated. The animals tested don't belong to the type of pet cats and dogs. All do not respond to the sugars tested (Table 2), to aspartame,

Table 2 Gustatory responses in cats and dogs of various compounds sweet to humans.

Compounds	Sweetness potency in humans (on a molar basis)	*Felis domestica*	*Canis familiaris*
Carbohydrates			
D-Fructose	0.5	–	–
D-Sucrose	1	–	–
Dipeptides derivatives			
Aspartame	170	–	–
Neotame	11 000	–	–
Miscellaneous			
Thaumatin	100 000	–	–
Magap	21 000	–	–
Sucralose	1160	–	–
Saccharine	215	–	–
Acesulfame-K	150	–	–
Na-cyclamate	17.6	–	–
Guanidine derivatives			
Lugduname	230 000	–	–
Carrelame	200 000	–	–
Sucrononate	200 000	–	–
Sucrooctate	162 000	–	–
Amino acids			
Glycine	0.15	–	–
D-Leucine	1.2	–	–
D-Threonine	0.28	–	–
D-Asparagine	2	–	–
D-Phenylalanine	3	–	–
D-Tryptophan	30	–	–
L-Proline	0.25	–	–

neotame, thaumatin, and other miscellaneous compounds and don't prefer the guanidine derivatives. The results with the sugars in dogs are not in agreement with other authors [17,18], but Kare [19] mentioned previously that "there was substantial individual variation in dogs". Maybe there exists a relationship to the daily diet of the individual dog, or we have—as in mice [20]—genetic variation among inbred dog subspecies/strains in taste responses to several sweeteners. We applied concentrations in the range obtained in taste experiments with humans and pigs and in some cases we offered a two- and four-fold higher concentrated solution. It should be noted that among the seven amino acids tested (Table 2) none was positive in cats and dogs, although all are known to be perceived as sweet to humans.

But, for instance, if we consider another carnivorous species—bears—it is known that they consume considerable amounts of sweet fruits and even honey. Maybe this fact is an indication that bears are not a true carnivorous species like all felidae.

In the year 2001, I ascertained gustatory responses from kangaroos, especially from a group of ten swamp wallabies (*Wallabia bicolor bicolor*), which originated from the southwestern region of Australia.

Their origin can be traced back to about 130 MYA with *Henkelotherium guimarotae* (Fig. 1), the oldest species known from the time between Jurassic and Cretaceous [21].

These new data with the wallabies show that they respond to six natural sugars (D-glucose, D-fructose, L-sorbose, D-maltose, D-sucrose, D-raffinose), but not to D-galactose and D-lactose (Table 3). When I tested the naturally occurring polyols in the marsupials, I found that they respond

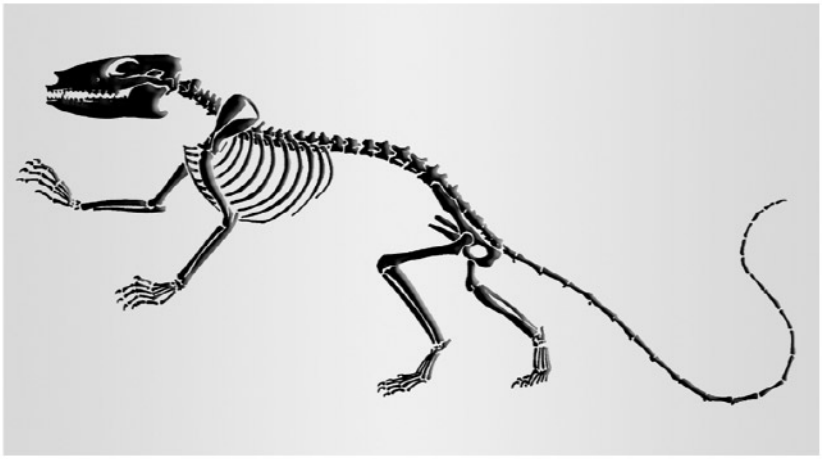

Fig. 1 *Henkelotherium guimarotae*, the oldest-known marsupial fossil.

Table 3 Gustatory responses of kangaroos to natural sugars and polyols.

Compounds	Sweetness potency in humans (on a molar basis)	*Wallabia bicolor bicolor*
Monosaccharides		
D-Galactose	0.2	–
D-Glucose	0.25	+
D-Fructose	0.5	+
L-Sorbose	0.25	+
Oligosaccharides		
D-Lactose	0.33	–
D-Maltose	0.33	+
D-Sucrose	1	+
D-Raffinose	0.25	+
Tetrols		
DL-Threitol	0.25	+
Erythritol	0.25	+
Pentols		
D-Arabitol	0.25	+
Ribitol	0.25	+
Xylitol	0.3	+
Hexols		
Mannitol	0.25	+
Sorbitol	0.25	+
Galactitol (Dulcitol)	0.25	+

positively to all tetrols, pentols, and hexols tested (Table 3) but in very high concentrations (between 0.125–1.0 mol/L).

The fact that kangaroos show no responses to dipeptide based derivatives [neotame, superaspartame, ASPE (*N*-α-L-aspartyl-D-serine propyl ester), aspartame, ASME (*N*-α-L-aspartyl-L-(*O*-tert-butyl)serine methyl ester), ampame], to phenylurea derivatives [CAMPA (*N*-(4-cyanophenylcarbamoyl)-(*RS*)-3-amino-3-(3,4-methyl-enedioxyphenyl)propionic acid), suosan], to guanidine

sweeteners [lugduname, carrelame, sucrononate, sucrooctate] and to other miscellaneous artificial sweeteners tested [magapame, sucralose, NHDHC (neohesperidine dihydrochalcone), saccharine, acesulfame-K, Na-cyclamate] as well as to some naturally occurring complicated sweeteners [thaumatin, stevioside, glycyrrhizic acid], strengthens the idea that the ability to taste artificial sweeteners and more generally noncarbohydrate sweet compounds is a link to a phyletic trend signaling a major change in the sweet taste receptors of more recent animal species.

The first time such a major difference was found was with thaumatin. This naturally occurring protein elicits an intensely sweet taste in humans and all other catarrhine primates, but no response at all in prosimians and South American platyrrhine primates [22]. Later we ascertained that the "thaumatin feature" should be a basic one since we found two dipeptide derivatives (i.e., aspartame [23] and neotame) displaying the same effect of separating the order of primates at the same intersection line as thaumatin (Fig. 2).

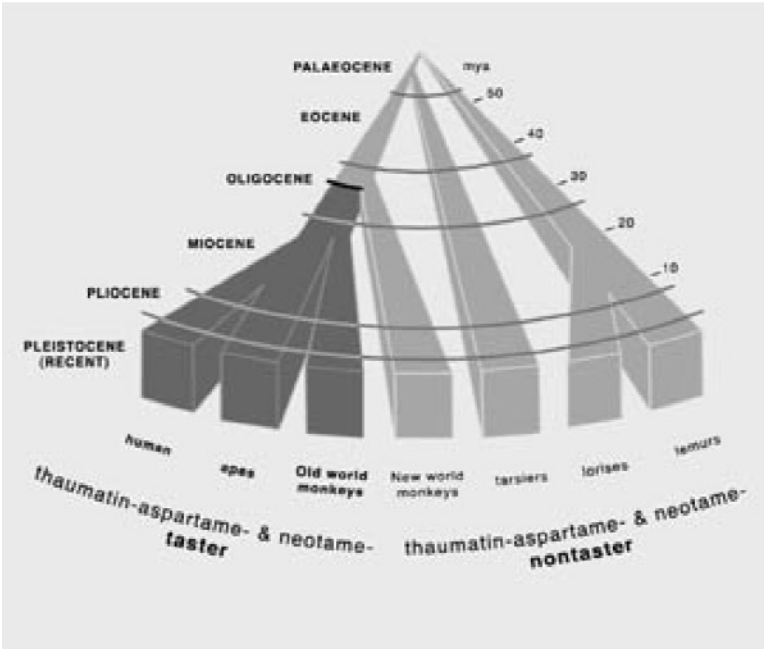

Fig. 2 The radiation of thaumatin-, aspartame- and neotame-taster from non-taster within the Order Primates around 37 MYA.

Now again, with kangaroos (originated about 130 MYA), which show no positive responses to these three same compounds, it is observed once more that animals that evolved before the Oligocene (about 37 MYA) are not able to taste thaumatin, aspartame, and neotame. The receptor modification [24] that allows higher animal species to taste the complicated artificial sweet substances must have then appeared in the Eutheria, with the more highly evolved mammals from the Lower Cretaceous (i.e., at about 100 million years ago). Since animal sweetness receptors were not designed to taste artificial sweeteners, the question of the advantage of this major modification of their sweetness receptors is still to be elucidated. Additional efforts, in studying comparative gustatory physiology, could be thus helpful in clarifying the evolution of the mammalians in the animal kingdom.

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